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Filipa da Maia Domingues Paciência

Dissertação de Mestrado
Mestrado em Biologia da Conservação

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Abstract

Defining Keystone Plant Resources (KPRs) has been a difficult task amongst researchers. The most common parameters to describe a KPR relate to the impact of the latter on vertebrate assemblages, their fruit abundance and reliability and their importance during periods of fruit scarcity.

This study, aims to fill a gap in the knowledge of *Marcgravia longifolia* ecology. This liana species is present in the Neotropics, and has the particular characteristic of producing fruits throughout its trunk, from low levels to the top. Therefore, we proposed it as a candidate KPR, since it can feed a wide range of vertebrates at different forest strata. The research was conducted at the Estación Biológica Quebrada Blanco (EBQB), in the Peruvian Amazon. Focal observations on different *Marcgravia longifolia* individuals revealed visitations by 17% by the bird species assemblage that exists at Quebrada Blanco (with approximately 324 species). When analyzing only species that actually fed on *Marcgravia longifolia* fruits, this percentage was still significant (14%). Additionally, phenology records showed that this species produced a high amount of fruits (ranging from 1516 to 5706 fruits per individual), while simultaneously having flowers available (with nectaries providing nectar). Fruits were shown to carry a high level of sugar, proteins and lipids, which potential makes them a very important resource for vertebrates in the community. Curiously, fruits also contained a considerable amount of tannins and phenols. These might constitute deterrents for vertebrate consumers of *M. longifolia* that are not efficient seed dispersers.

Recognizing KPRs is of extreme importance when projecting or monitoring conservation areas, as well as for the creation of new policies and guidelines. However, it is important to highlight that the keystone status is not restricted to species, but instead context-dependent, with the community structure being the main responsible for this categorization.

Key words: *Marcgravia longifolia*, Keystone Plant Resource, frugivory, Peruvian Amazon.

Sumário

A definição de recursos-chave não tem sido uma tarefa fácil entre investigadores. No entanto os parâmetros mais utilizados para a descrição de recursos-chave, estão relacionados maioritariamente com o seu impacto na comunidade de vertebrados, a sua abundância e fiabilidade na época de frutificação e finalmente com a sua importância durante períodos de seca e escassez alimentar.

Este estudo visa o preenchimento de uma lacuna sobre a ecologia da *Marcgravia longifolia*, uma espécie de liana Neotropical que possui a característica peculiar de produzir infrutescências com frutos ao longo de todo o tronco desde os níveis mais baixos até à canópia, assim como inflorescências e néctar. Assim sendo, propõe-se esta liana como uma candidata a recurso-chave, devido à sua particularidade de poder ser utilizada por um grande leque de vertebrados que vivem em diferentes estratos da floresta tropical.

O único estudo efectuado com base nesta espécie pertence a Tirado Herrera *et al* (2003) onde foram identificados os seguintes consumidores e dispersores desta liana: duas espécies de aves da família Pipridae, *Dixiphia pipra* e *Lepidothrix coronata* e três espécies de primatas, *Callicebus cupreus*, *Saguinus mystax* e *Saguinus nigrifrons*. Foi também identificado um polinizador, *Anoura caudifer*, uma espécie de morcego pertencente á subfamília Glossophaginae, que se alimenta do néctar presente nos nectários das inflorescências (as flores florescem apenas de noite, fechando pela manhã). Esta investigação, foi efectuada na Estación Biológica Quebrada Blanco (EBQB), na Amazónia Peruana, tal como o trabalho de campo desenvolvido nesta tese. A estação, dirigida pela DPZ (Deutsche Primatenzentrum), possui cerca de 100 hectares e é composta por um sistema de trilhos desenvolvidos aquando da sua fundação. A vegetação é dominada maioritariamente por floresta primária de terra-firme e por pequenas zonas pantanosas.

O trabalho de campo, desenvolvido entre Outubro de 2013 a Janeiro de 1024, teve como tarefa primária a localização e marcação dos vários indivíduos de *Marcgravia longifolia* com o auxílio de um GPS (alguns indivíduos eram previamente conhecidos devido ao estudo efectuado em 2003). No total foram identificados 52 indivíduos de *Marcgravia* sendo que entre eles, 3 pertencem a outra espécie que não *M. longifolia* e por isso não serão

analisados no seguimento deste trabalho, permanecendo assim com um total de 49 indivíduos. Esta espécie de liana, possui um período de frutificação entre Setembro e Dezembro, onde a abundância de frutos e flores é mais elevada. No entanto apresenta frutos durante a maior parte do ano, incluindo a época seca.

Para comprovar a sua importância como recurso-chave, e para se obter mais informação sobre os possíveis visitantes e consumidores desta espécie, foram efectuadas observações focais entre sete lianas de *Marcgravia longifolia*. A escolha dos indivíduos teve por base as sua acessibilidade e observação, tal como a visibilidade dos frutos. As observações foram efectuadas entre as 6 horas da manhã e as 12 horas da tarde, alternando os horários entre as diferentes lianas. Os resultados obtidos das observações focais foram comparados com um inventário de aves efectuado por Lars Pomara em 2006 na zona de Quebrada Blanco, onde cerca de 324 espécies foram identificadas. Assim, verificou-se que 17% destas aves eram visitantes da *M. longifolia*. Ao analisar esta percentagem relativamente aos consumidores (pois nem todos os visitantes consumiram frutos durante a sua visita) obteve-se um resultado de 14%, traduzindo-se num valor bastante significativo da comunidade de aves que se alimenta desta liana.

Adicionalmente, trabalho fenológico realizado durante o estudo, onde inflorescências e infrutescências foram contabilizadas, demonstrou que diferentes indivíduos de *Marcgravia longifolia* são capazes de produzir uma elevada quantidade de frutos (entre 1516 a 5706 frutos por individuo). Relativamente aos frutos, foram efectuados testes sobre a quantidade de açúcar existente nos mesmos através de um refractómetro manual (0 – 32% Brix), tendo-se obtido uma média de 25% (desvio padrão = 2.3) num intervalo de 18.5% - 29.2%, o que revela um elevado nível de açúcar. Estes resultados corroboram um estudo efectuado sobre frutos consumidos por primatas e morcegos também na EBQB em que foi demonstrado que os frutos de *M. longifolia*, em comparação com outros analisados, possuem não só elevadas quantidades de açúcar mas também de proteínas e lípidos (Ripperger *et al*. 2014) revelando-se assim um importante recurso para a comunidade. Curiosamente, na análise efectuada foi também demonstrado que estes frutos são detentores de taninos e fenóis, especulando-se sobre a sua função de dissuasão de possíveis consumidores que não tenham um papel de dispersor desta planta. Aliado ao valor nutritivo, estes frutos possuem também um elevador teor em água, pois ao comparar o seu peso fresco com o peso seco (medido após os frutos serem deixados dois dias em sílica) verificou-se que houve uma redução do peso para menos de metade.

Adicionalmente aos estudos acima referido, foram também colectadas amostras fenológicas (folhas, frutos, análise da presença látex) dos hospedeiros utilizados pela *Marcgravia longifolia*. No entanto, vários hospedeiros devido à sua altura, canópias com pouca folhagem ou devido à presença de muitas epífitas, a recolha de amostras não foi possível, permanecendo alguns indivíduos sem identificação. Assim sendo, no total foram identificados 36 hospedeiros sendo o género mais comum pertencente à família Lecythidaceca e ao género *Eschweilera*. Todas as análises efectuadas tiveram por base o género e família para evitar conflitos taxonómicos de espécies entre botânicos. Para analisar se existia preferência de hospedeiros por parte da *M. longifolia* compararam-se os seus hospedeiros com um inventário efectuado por Dávila & Rios (2006) em que dois hectares da EBQB foram exaustivamente catalogados ao nível da população de plantas. Estes dois hectares foram extrapolados visto que eram representativos de floresta primária e áreas não inundáveis (habitat onde todos os indivíduos de *Marcgravia longifolia* foram identificados). Após análises efectuadas, a probabilidade de aceitar a hipótese nula (sem preferência de hospedeiro) era de 75% tendo em conta o género e 42% tendo em conta a família. Este resultado indica que a *M. longifolia* cresce em hospedeiros de acordo com a maior ou menor disponibilidade dos mesmos no ecossistema. Este resultado está de acordo com o que se observou em campo, pois Eschweilera estava entre os géneros mais comuns na EBQB.

Assim sendo, devido a todas as características mencionadas anteriormente, a liana *Marcgravia longifolia*, poderia ser uma candidata a recurso-chave. Um estudo a longo prazo e mais aprofundado seria necessário para se provar tal categorização, no entanto este trabalho pode ser visto como um estudo preliminar sobre uma espécie de liana que todavia é bastante desconhecida.

O reconhecimento de recursos-chave é de alta importância para o delineamento ou monitorização de áreas protegidas, tal como para a criação de novas políticas de conservação. Neste caso, é importante o conhecimento e informação sobre esta espécie de liana, já que os hospedeiros identificados onde a mesma cresce, são na sua maioria árvores que são abatidas pela indústria madeireira. É também frequente, durante operações realizadas por madeireiros o corte de lianas das árvores que vão ser abatidas no futuro, de modo a preservar o valor comercial da madeira (Putz 1991), afectando possivelmente indivíduos de *Marcgravia longifolia*.

É no entanto relevante mencionar que o *status* de recurso-chave não é uma propriedade intrínseca de uma espécie mas sim dependente do contexto ecológico em que se insere. Assim, o ecossistema em que a *Marcgravia longifolia* esta integrada irá definir a atribuição desta categoria de recurso-chave, e o papel que esta liana pode exercer na sua comunidade pode ser alterado de acordo com alterações na comunidade em que se insere.

Palavras-chave: *Marcgravia longifolia*, recursos-chave, frugivoria, Amazonia Peruana.

1. Introduction

Keystone species can be defined as `animal or plant species with a pervasive influence on the community composition' (Howe & Westley 1988). The identification of keystone species, based on quantifiable traits, is of high importance for developing effective conservation policies (Power *et al*. 1996). Reaching a consensus on how a keystone resource is defined has proven difficult amongst researchers (Gautier-Hion & Michaloud 1989; Terborgh 1986a; Peres 2000; Stevenson 2005). This is especially true for plant species, due to their complex role within ecosystems. Nevertheless, it has become widely accepted that selective removal of keystone resources may considerably reduce forest carrying capacity for frugivores and seed predators (Whitmore 1990). Tropical keystone resources include fruits, seeds, flowers, nectar, and bark produced by a small set of species that provide nutrients to a large fraction of the vertebrate assemblage (Terborgh 1986 a,b). Key Plant Resources (KPRs) definitions have varied between those highlighting only resource redundancy (e.g. Leighton & Leighton 1983, White 1994), definitions including redundancy and reliability (Terborgh 1986 a,b) only resource abundance (Paine 1966, Power & Mills 1995, Power *et al.* 1996) and lastly those mainly focused on post-removal effects (Bond 1993, Howe & Westley 1988, Lawton 1993, Mills *et al.*1993). Resource redundancy is defined as the degree of synchronization with other plant species that serve as food resources to the animal community, which can turn a KPR candidate into a highly important species depending on the availability of the other plant species. The second definition includes not only resource redundancy but also reliability, a measure of predictability that a plant will fructify in a certain period. Resource abundance gives emphasis only to the degree of productivity (e.g. fruits, flowers, nectar) by a plant species, while post-removal effects are understood as the impacts in the ecosystem triggered by the elimination of a keystone species.

In the present work, I investigated whether *Marcgravia longifolia* could constitute a keystone resource. This liana is the only one amongst the family Marcgraviaceae with the peculiar characteristic of providing inflorescences (with nectar) and infrutescences over a broad vertical range, namely from the ground to the canopy (at around 20 -25 meters high).

Vertical patterns in the distribution of bird species (e.g. Walther 2002; Jayson & Mathew 2003) primates (e.g. Buchanan-Smith *et al.* 2000; Heymann *et al*. 2002) and other mammals (e.g. Vieira & Monteiro 2003; Pereira *et al*. 2010) are well-known. Therefore, *Marcgravia longifolia* can address a broad spectrum of nectarivorous and frugivorous species. Nevertheless, a thorough investigation of the ecology of this species is required in order to confirm this hypothesis.

Marcgraviaceae, is an exclusively Neotropical plant family with around 140–150 species, that is divided in lianas, and hemiphytic and epiphytic shrubs belonging to the Order Ericales. The *Marcgravia* genus, with circa 60 species, is native of the Northwest South America (Peru and Colombia), Costa Rica, Panama, South Mexico and Antilles, with its distribution being affected by both humidity and altitude (Giraldo-Cañas 1999, Dressler 2011). *Marcgravia* individuals root in the forest floor, and the majority of species have their inflorescences almost exclusively, high up in the canopy, which explains the lack of knowledge on this genus. Its individuals have a dimorphic growth: leaves of young plants are attached to the bark of the host tree trunk but, when adults, produce shoots projected towards open air. These branches, at their terminus, produce inflorescences that later become infrutescences (Tschapka & von Helversen 1999). *M. longifolia* foliage is exclusively produced in the canopy.

While in other genera of the family like *Souroubea*, *Ruyschia*, and *Norantea*, every flower has its own nectary, the inflorescence of *Marcgravia* consists of a ring composed of fertile flowers surrounding a number of nectaries derived from bracts and fused with sterile flowers (Dressler 2004). These nectaries are normally present in proportions of 4 to 6 units per inflorescence. The opening of their flowers always occurs after dusk, revealing rings of ephemeral white stamen that are shed before daybreak. The peculiar architecture of *Marcgravia*'s inflorescences has attracted attention amongst ecologists since a long time. Ornithophily was frequently mentioned to be the predominant mode of pollination for *Marcgravia*, with Belt (1874) being the first one to document hummingbird visits to *Marcgravia nepenthoides*, and later, Bryant (1905) confirming these observations in another species - *Marcgravia umbellata*. However, since the majority of *Marcgravia* species only open their flowers during night, one would expect that their pollinators would be nocturnal. This was suggested by Vogel (1958) and finally confirmed by Sazima &

Sazima (1980) who observed bats from the Glossophaginae subfamily feeding on *Marcgravia mynostigma* nectar. Later, Tschapka & von Helverson (1999) identified a broad spectrum of humming birds and other nectar-feeding birds as flower visitors of different *Marcgravia* species during the day. During the night, Glossophaginae bats were shown be the main pollinators of *Marcgravia* species and also an opossum species (*Didelphis marsupialis*) was described as pollinator of *Marcgravia nepenthoides*.

Concerning frugivory, there are no studies focusing on *Marcgravia* and its consumers. In this thesis, I aimed at contributing to filling this gap in the knowledge of this species. The study took place at Estación Biologica Quebrada Blanco (EBQB), where an extensive research background regarding primates in this area is available (Heymann 1996; 1998; Knogge *et al*. 2003; Culot *et al*. 2010; Kupsch *et al*. 2014) being *M. longifolia* known to constitute a food resource for tamarins and titi monkeys at this site (Tirado Herrera *et al*. 2003; Culot *et al.* 2009; Ripperger *et al.* 2014). To date, the only study focusing on *Marcgravia longifolia* was performed by Tirado Herrera *et al.* (2003), at EBQB, where the following consumers and dispersers for this liana were identified: two manakins, *Dixiphia pipra* and *Lepidothrix coronata* and three primate species, *Callicebus cupreus, Saguinus mystax and Saguinus nigrifrons,* previously known as *Saguinus fuscicollis nigrifrons* (Matauschek *et al*. 2001). Furthermore, a pollinator was also identified, a bat from subfamily Glossophaginae: *Anoura caudifer*. An additional study performed by Ripperger *et al.* 2014, revealed that two frugivorous bats belonging to the subfamily Stenodermatinae (*Rhinophylla pumilio* and *Rhinophylla fischerae*) were also frequent consumers of *Margravia longifolia*'s fruits. Finally, data collected during 1995, 2000, and 2006 on tamarins feeding behavior, showed that, depending on the year, *Marcgravia logifolia* was amongst the top three species consumed from August to November (Culot 2009). In tropical ecosystems, seed dispersal is carried out mostly by animals like birds, bats, and primates. Bird species play a fundamental role as it was suggested that in most rainforest ecosystems over 70% of woody plant species that bear fleshy fruits are dispersed by these vertebrates (Willson *et al.* 1989; Şekercioğlu 2006). On the other hand, primates might constitute 25 to 40% of the vertebrate frugivore biomass (Eisenberg & Thorington 1973) in tropical forests, where some species are also involved in the dispersal phenomena. It should be considered, though, that bat-dispersed seeds are more likely to reach highly disturbed areas that lack perching and nesting sites rather than bird and primate dispersed seeds.

By conducting focal observations on different *Marcgravia longifolia* individuals, I aimed at increasing the list of known frugivores feeding on this plant. By doing this, I could also infer on which animals could constitute putative dispersers of *Marcgravia longifolia*. Additionally to focal observations, phenology work was performed in order to obtain more information about this rather unknown plant species. Information was gathered on inflorescences and individual flowers, infructescences and fruits. Furthermore, the physical characteristics of *Marcgravia* plants and their respective hosts were annotated and a particular effort was done to identify all host individuals in order to investigate whether are selected randomly or not.

The following objectives have guided this thesis:

1. Investigate whether *Marcgravia longifolia* is a candidate for a KPR.
2. Observe the spectrum of animal species feeding on *Marcgravia longifolia*, and whether consumers respond to the availability of *Marcgravia longifolia* fruits.
3. Determine whether there is habitat host preference of *Marcgravia longifolia*.

2. Materials & Methods

2.1 Study area

The study was conducted from October 2013 to January 2014 at the Estación Biologica Quebrada Blanco (EBQB), located in the northeastern Peruvian Amazon (4°21'S 73°09'W), 90 kilometers south-southeast of Iquitos. The field station is managed by the German Primate Center (DPZ) and is located on the Blanco river, a small whitewater river running east to west that drains into the Rio Tahuayo, a black-water river which empties in the Amazon (Garber 1986). The field station is composed by a trail system and primary terra-firme forest dominates the 100 hectares of study area. The southern part includes a patch of 3.5 hectares covered by anthropogenic secondary forest that belongs to a 15 hectares area of buffalo pasture abandoned and regenerating since 2001 (Culot *et al.* 2010).

The majority of the vegetation in the study area is high-ground, non-floodable rain forest interspersed with small swampy areas. (Encarnación 1985)

Figure 1 - Localization of the DPZ field station in the Peruvian Amazon.

The site has a short dry season from July to September. The wet season initiates in October, with increasing rainfall observed until January and its peak occurring from February to May (Garber 1993). Weather conditions were measured at the nearest meteorological station (Tamshiyacu, ca.40 km northwest of the EBQB) and are presented in Fig.2.

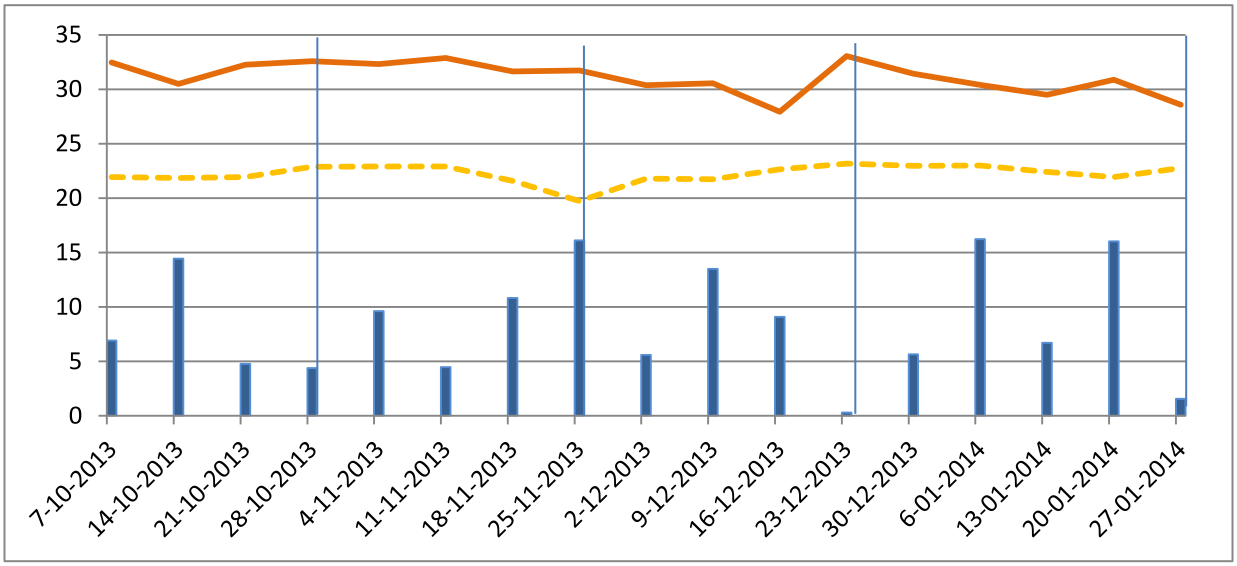

Figure 2 - Weekly mean Precipitation (bars) and weekly mean Temperatures (Maximum - filled line, minimum - dashed line) from October 2013 to January 2014 at the meteorological station in Tamshiyacu, Peru.

2.2. Data collection methods

2.2.1 Population Survey

A survey of the area of study was done with the aim of identifying as many of *Marcgravia longifolia* individuals as possible, although several individuals were already known from a previous study (Tirado Herrera *et al*. 2003). Systematic surveys were made along the trail system to detect additional individuals.

For all individuals, the following variables were collected:

- Location (GPS position with a GPSmap 76CSx Garmin).
- Diameter at Breast Height (DBH) of the *Marcgravia* individual.

- Diameter at Breast Height (DBH) of the *Marcgravia* host tree.
- Height of the *Marcgravia* individual.
- Botanical samples of the host tree: leaves, fruits, bark. The presence or absence of latex was observed. Photographs were taken in order to assist in host identification.

Samples were later identified to at least genus level, by Ricardo Zarate Gómez, a botanist from “Instituto de Investigaciones de la Amazonia Peruana” (IIAP).

Furthermore, calculations on *Marcgravia longifolia* distribution within the study area were performed. These analyzes included the Nearest Neighbor Index (NNI), to estimate sample clustering and the Minimum Convex Hull (MCH), to calculate the area over which this species is distributed.

The Nearest Neighbor Index (NNI) is a tool for analyzing if a set of points is randomly, regularly distributed or clustered by using the distance between each point and its closest neighbor for its determination. It is calculated by dividing the observed mean distance to the closest neighbor by the expected mean distance between points. The values of NNI range between two theoretical extremes, 0 and 2.1491. With increased proximity between two points, NNI will tend to 0, since the average nearest neighbor distance decreases. The closer NNI gets to 1, more randomness in points will be observed, and when it approximates to 2 there is a regular distribution between points. The null hypothesis states that features are randomly distributed, and besides the probability of the null hypothesis it was calculated as well a Z-score value. If data are normally distributed, approximately 95% of the data should have Z-score between -2 and +2. If Z-score does not fall within this range the distribution may be less typical, indicating clustering if negative while a positive score points to dispersion or evenness.

2.2.2. Visitors of *Marcgravia longifolia*

Based on accessibility and observation conditions as well as fruit availability, seven *Marcgravia longifolia* individuals were selected for surveillance of animal visits. The focal observations were carried out during 25 days, totalizing 83 observation sessions with a total effort of approximately 255 hours. This task was performed with the aid of binoculars (DCF – CS Pentax 10x42) to facilitate identification of species.

All observations were done between 6:00 in the morning when bird activity was at its peak, being extended until 12:00 afternoon. Shifts of two hours were performed (few times of one and a half hour) for each *Marcgravia longifolia* individual. Occasionally, simultaneous observations of three individuals were carried out with the aid of two field assistants. Of note, the observation effort was unequal between *Marcgravia* individuals as fruit availability differed considerably between them.

Since during fieldwork it was observed that not all visits implied fruit consumption, two different categories ("Consumers" and "Non consumers") were distinguished in the data analyzes.

Information on all observed visits was annotated regarding the following variables:

- Day
- Hour
- *Marcgravia longifolia* individual observed
- Time of arrival
- Species
- Sex
- Number of individuals
- Number of fruits eaten
- Canopy height
- Time of departure

Visits were defined as all physical interactions between animals and a *Marcgravia* individual. A consumption event was defined as an individual arriving at the tree and picking at least one fruit.

Identifications of species were carried out based on three field guides: Clements & Shany (2001), Ridgely & Greenfield (2001) and Hilty & Brown (1986). Species that could not be identified were denominated as unidentified bird (UB), being distinguished by differentiating features that were annotated regarding morphology and behavior.

2.2.3 Phenological data

2.2.3.1. Inflorescences & Infructescences counting

Seven *Marcgravia longifolia* individuals were selected based on their accessibility and visibility for counting the number of inflorescences (plus the number of individual flowers and nectaries) and infructescences (plus the number of individual fruits). All counts were done until 3 m height. The fruits were divided in two categories: unripe fruits (U), when the fruit was still inside the brownish husk and ripe fruits (R) when the husk had dehisced and the typical intense red fruit pulp was exposed. This task was normally performed once a week and two results are displayed: results from the first week of counting, in order to have an approximation of the maximum plant productivity and another result with the mean number from the total counting during the study.

Concerning the crop-size (total number of fruits on a plant), the value obtained for each *Marcgravia longifolia* was extrapolated from the total number of fruits counted in 1 m height, multiplying this number by the total height of the liana.

2.2.3.2. Fruit mass and chemical composition

To determine their fresh mass, fruits were collected and weighed on a scale (Almasa model MT-5 20g/0.001g). Afterwards, the fruits were left 2 days to dry in a small box containing silica and their dry mass was measured.

Sugar concentration was measured by squeezing fruits into the Manual Hand-held Refractometer (Krüss HRT32 - 0-32 % Brix) which was pointed to a natural or artificial light source and values were recorded.

2.2.3.3 Fruit loss monitoring

Net traps were placed at the base of three *Marcgravia* individuals (ID 2, 21, 32) to estimate fruit loss by each liana. The nets had an area of circa $5m^2$ and were placed in order to cover the area projected from the *M. longifolia* “canopy” to the ground level. Each net was checked daily, and fruits were counted at the beginning and end of each day. Nets were cleared after each counting. Traps were placed during the entire study period, from October to January, totalizing an effort of 49 days of fruit counting.

2.2.4 Host specificity

After *Marcgravia* host identification, the list of host species was compared to a list of plant species available in the study area. The latter was extrapolated from an exhaustive inventory performed by Dávila & Ríos (2006) in two hectares of the study area that was exclusively composed of terra-firme forest. To date, *Marcgravia longifolia* was only found in non-floodable areas, thus the use of the inventory data is justified. To minimize potential errors introduced through plant identifications by different botanists (Dávila and Ríos in 2006, Zarate in this study), I used only genera and families in the analyzes.

All calculations in this section were based on the inventory mentioned above.

2.2.4.1 Host diversity in the study area

Species diversity is an attribute of a biological community and can be measured by methodologies. Species richness is the oldest and the simplest concept of species diversity, and measures the number of species in a community (Krebs 2014). Heterogeneity is an additional way to measure species diversity and was first applied by Good (1953). This measurement contains two separate components, species richness and Evenness, with the latter being measured separately, with Lloyd & Ghelardi (1964) being the first authors to suggest this concept. For calculating heterogeneity different formulas can be employed, while some give more emphasis on rare species in a sample (Shannon-Wiener function and Brillouin’s Index), others focus on common species, like Simpson’s Index and Reciprocal of Simpson's index. The choice of what measures should be used is related to the research focus, whether dominant species or rare species are emphasized in the community. In the current work, both estimations will be presented.

Regarding evenness, it is known that most communities (plants and animals) contain few dominant species and several relatively uncommon species. Evenness measures attempt to quantify this unequal representation against a hypothetical community (Krebs 2014) and it is considered high when it varies near 1. Different indexes can be used to measure evenness. Smith and Wilson's index is one of them, and it is independent of species richness and sensitive to both rare and common species in a community (Smith and Wilson 1996). Camargo's index (E') is unaffected by species richness and like Simpson's E index it is relatively unaffected by the rare species in the sample (Camargo 1993). Once more, the index used will depend of the aim of the study, but in this thesis all measures will be calculated.

These estimations will be performed for both genera and family classes, using the inventory done by Dávila & Ríos (2006) which represents the possible hosts for *Marcgravia longifolia* individuals. For each genera and family calculations, two estimations were performed, one including all individuals from genera and all individuals from family and one calculation excluding the rare genera and rare families (defined as having only one individual present in the inventory). This exclusion is due to the low probability of *Marcgravia longifolia* colonizing one of these rare individuals.

2.3 Software

All data was entered in Microsoft Excel (Microsoft Excel XP/2000) for subsequent statistical analyzes. All statistical tests, such as species richness, host specificity and rarefaction curves were run in Ecological Methodology version 7.2 by Charles J. Krebs. For graphic construction Microsoft Excel was employed.

The QGIS 2.2 Valmiera software was used for projecting the GPS coordinates from *Marcgravia individuals*, calculating the Nearest Neighbor Index (NNI), and the Minimum Convex Hull (aka Minimum Convex Polygon).

3. Results

3.1 Population survey

The grid displayed in Fig. 3, represents the area of study, divided by transects. All individuals are indicated according to their position: in total 52 *Marcgravia* individuals are shown, but as 3 individuals (in red) probably belong to a species different than *Marcgravia longifolia*, only 49 individuals (in blue) are considered for posterior analyzes. The GPS positions for each individual are displayed in the Appendix.

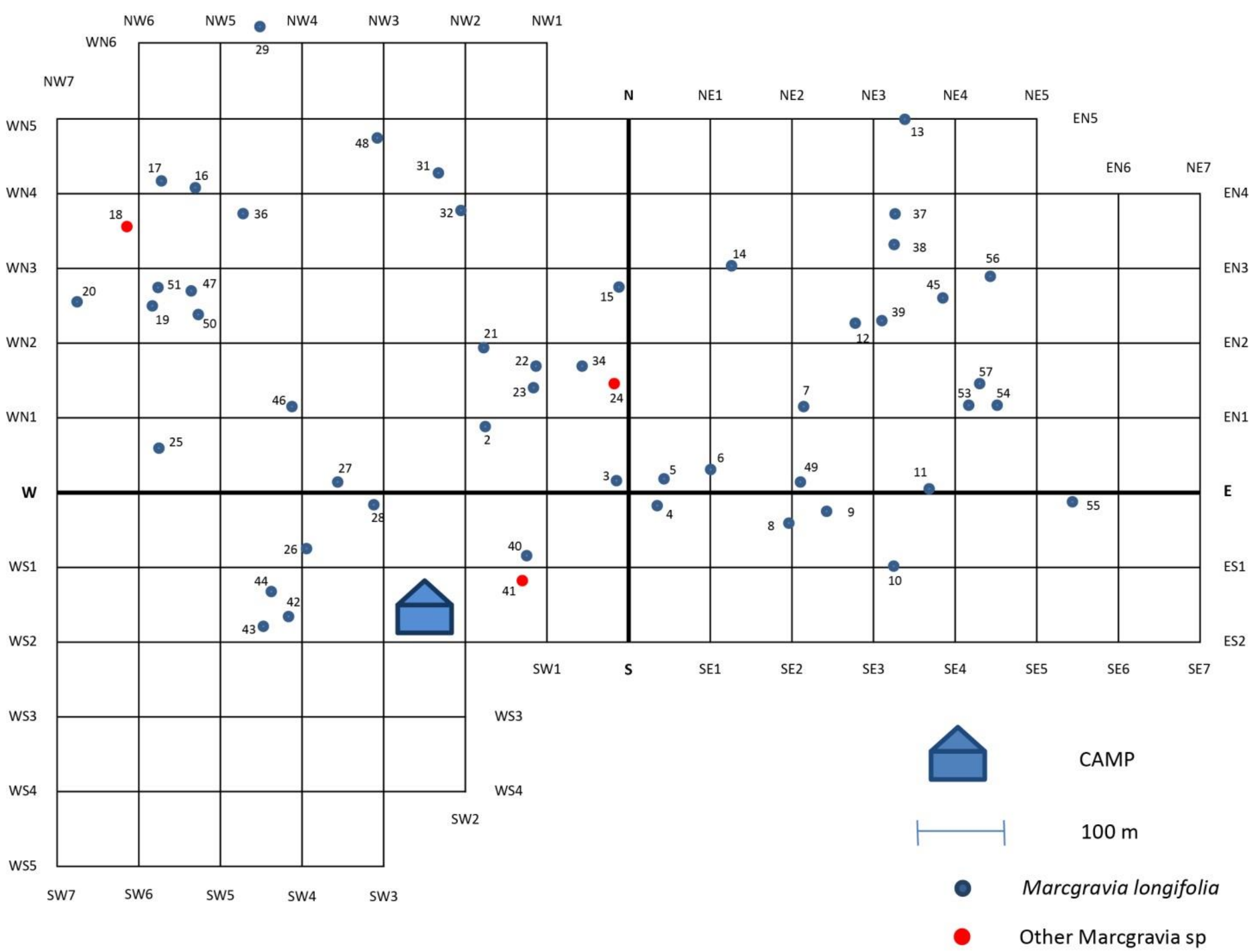

Figure 3 – Map grid of the field station with all *Marcgravia* individuals marked

3.1.1 Population analyzes

For *Marcgravia longifolia* population analyzes, the Nearest Neighbor Index was calculated for the total sample of *Marcgravia longifolia* (49 individuals). An NNI and a Z-score of 0.78 and -2.8, respectively, were determined for the entire population, which still indicates clustering of individuals (Table 1). Additionally, calculation excluding outliers from the population was performed, where a buffer zone was created and individuals positioned away from each other more than 100 meters were excluded. Outliers could influence the results since these points are exceptionally distant from the remaining and can be attributed to sampling errors. The resulting NNI was 0.69, which indicates a higher clustering.

Table 1 – Population Analyzes of *Marcgravia longifolia*

	Total sample	Excluding outliers
Observed mean distance	61.6	43.4
Expected mean distance	78.2	62.9
Nearest Neighbor Index	0.78	0.69
Number of individuals	49	42
Z-score	-2.8	-3.8
Minimum convex hull (hectares)	80.71	52.05
Ecological density	0.6	0.8

The Minimum Convex Hull (MCH) is the smallest area containing all set of points. Considering the total area of the study site (100 hectares) the aim was estimate *Marcgravia longifolia* population density. Density is an expression of the numerical strength of a species where the total number of individuals in all the quadrats is divided by the total number of quadrats studied (Curtis and McIntosh 1950). Hence, the MCH was estimated for the total sample (Fig. 4) and for the sample excluding outliers (Fig. 5) which resulted in an ecological density of 0.6 per ha and 0.8 per ha respectively, reflecting an inverse relationship, the smaller the area the higher the *Marcgravia* density. Since previous information indicates that inundated areas (southernmost part of the study site towards Quebrada Blanco) and secondary forest are not colonized by *Marcgravia longifolia*, using the entire study area would result in an inaccurate calculation.

Comparing the results of the MCH with the total study area (100 hectares), both estimations including all individuals and excluding outliers have a fine representation of the entire area. Therefore, the effort made during the field work for identifying *Marcgravia* individuals can be considered as representative of the total dimension of the field study.

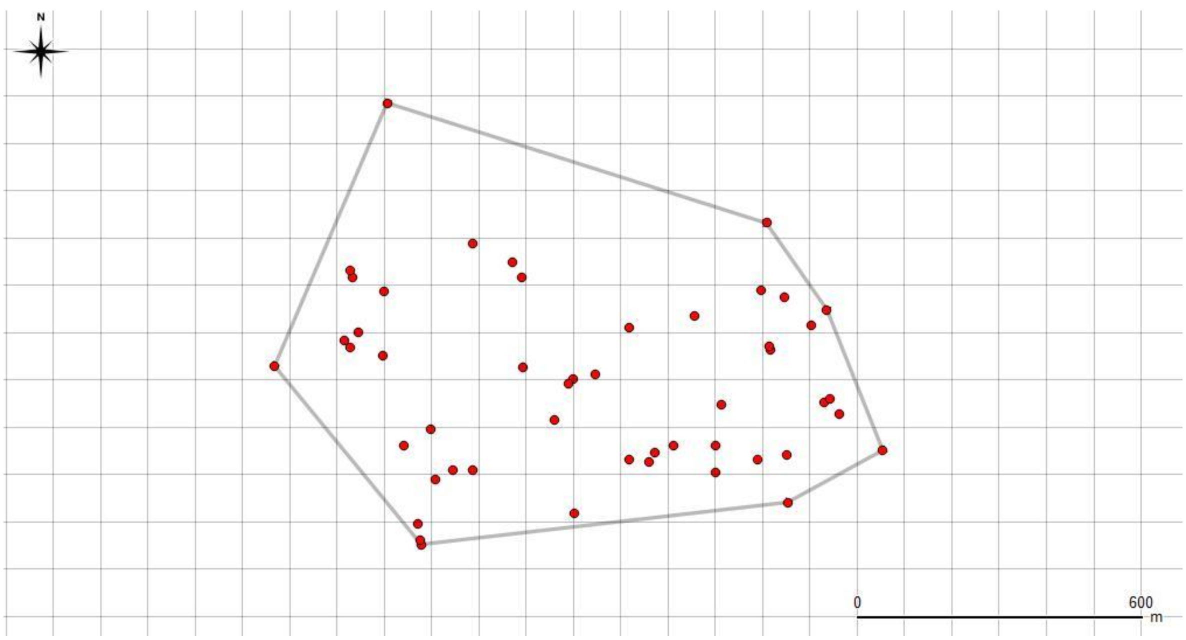

Fig 4 - *Marcgravia longifolia* population surrounded by the MCH

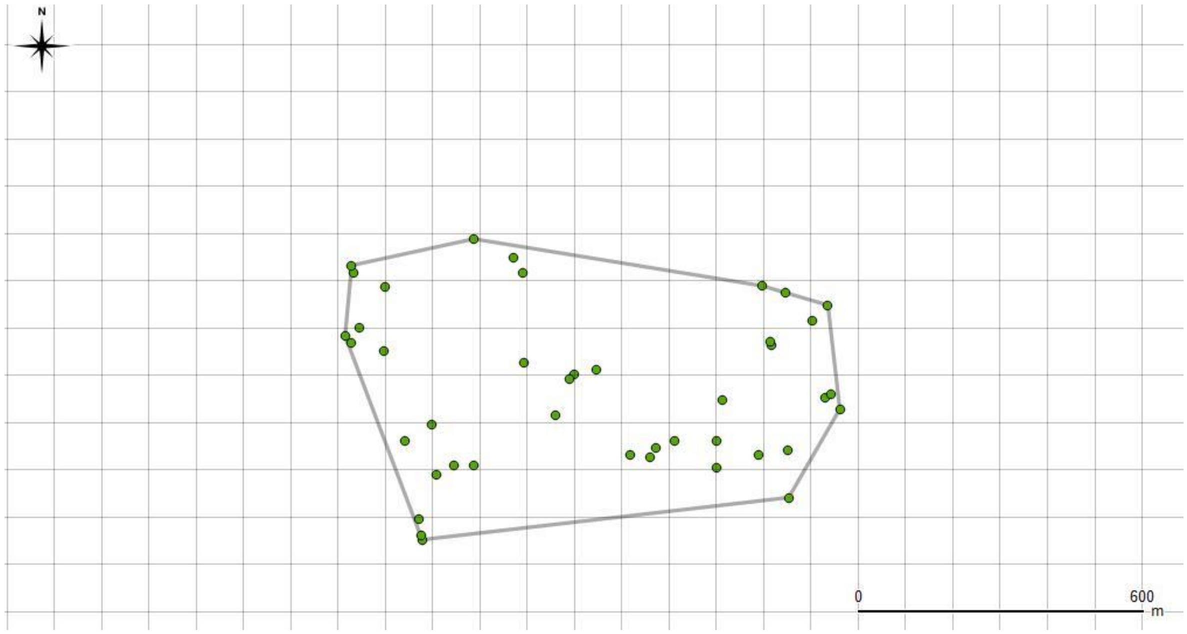

Fig 5 – *Marcgravia longifolia* population excluding outliers surrounded by the MCH

3.2 *Marcgravia longifolia* visitors

During 25 days of focal observations at 7 *Marcgravia longifolia* individuals, we observed a total of 60 different species of visitors from which 21 were unidentifiable bird (UB) species (Table 2). From the total number of visitors, only five species did not feed on the liana's fruits during the observations, limiting their behavior to perching or foraging at the host tree and/or liana. This represents a major increase in the list of consumers of *Marcgravia longifolia* from what was previously reported.

Table 2 - List of visitors identified during focal observations of *Marcgravia longifolia* individuals

Visitors	Dietary information
Campephilus sp	Insectivore
Capito auratus	Frugivore/small prey
Chlorophanes spiza	Frugivore
Cyanerpes caerulus	Nectarivore/frugivore
Cyanerpes cyaneus	Nectarivore/frugivore
Disglossa albilatera ⌂	Nectarivore/frugivore
Disglossa mystacalis ⌂	Nectarivore/frugivore
Dixiphia pipra	Frugivore
*Eubucco richardsoni**	Frugivore/insectivore
Euphonia chlorotica	Frugivore
Euphonia laniirostris	Frugivore
Euphonia minuta	Frugivore
Euphonia rufiventris	Frugivore
Euphonia saturata	Frugivore
Euphonia sp	-------------
*Heliodoxa aurescens**	Nectarivore/insectivore
Lamprospiza melanoleuca	Frugivore
Lepidothrix coronata	Frugivore
Lipaugus fuscocinereus ⌂	Frugivore/insectivore
Lipaugus vociferans	Frugivore/insectivore
Patagioneas plumbea	Frugivore
*Phaetornis philippi**	Nectarivore/insectivore
Pipra erythrocephala	Frugivore
Pipra rubrocapila	Frugivore
Pipra sp	-------------
Pipreola pulchra ⌂	Frugivore
*Pithecia monachus**	Frugivore/small prey
Pteroglossus sp 1	Frugivore/insectivore
Pteroglossus sp2	Frugivore/insectivore

*Saguinus mystax**	Frugivore/small prey
Saguinus nigrifrons	Frugivore/small prey
Tachyphonus surinamus	Frugivore/small prey
Tangara schrankii	Frugivore/small prey
Tangara sp	Frugivore/small prey
Tersina viridis	Frugivore/small prey
Thraupis palmarum	Frugivore/small prey
Tityra cayana	Frugivore/insectivore
Trogon curucui	Frugivore/small prey
Unidentified sp 1*, 2*,9*,10*	---------------------------
Unidentified sp 3,4,5,6,7,8,11,12,13,14,15,16,17,18,19,20,21	---------------------------
Xenopipo holochlora ⌂	Frugivore

* No fruits were consumed (except *Saguinus mystax* that was seen feeding before the period of focal observations start)

⌂ Distribution range does not match with EBQB location.

Fifty-seven of the visitors' species were birds, and considering that in the Quebrada Blanco area (where the field station is located) there are circa 324 bird species (inventory made by Lars Pomara in 2006); there is a representation of 17% of the bird assemblage visiting *Marcgravia longifolia*.

Figure 6 – *Lepidothrix coronata* at a *Marcgravia longifolia* individual.

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Figure 7 – *Saguinus nigrifrons* feeding on the fruits of a *Marcgravia longifolia*

Figure 8 – *Pipra rubrocapilla* female feeding on the fruits of a *Marcgravia longifolia*

3.2.1 Consumers & Non consumers

To compare the number of visits where feeding occurred or not, a graph was generated to summarize the data (Fig 9). One can observe that the majority of visits performed by animals at *Marcgravia* individuals resulted in fruit consumption. The only exception was ID25 where the majority of visits did not lead to fruit consumptions.

No relation was encountered between the number of fruits present at an individual and the number of visits (Fig 10). For instance, ID32 carried a high number of fruits while being one of the less visited individuals.

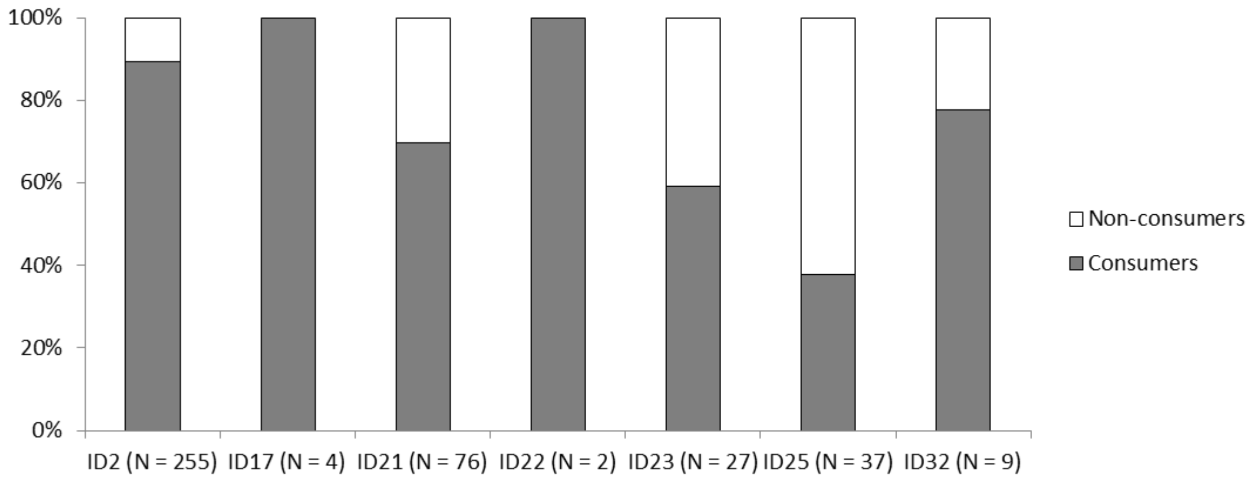

Figure 9 – Representation of consumers and non-consumers in different *Marcgravia longifolia* individuals

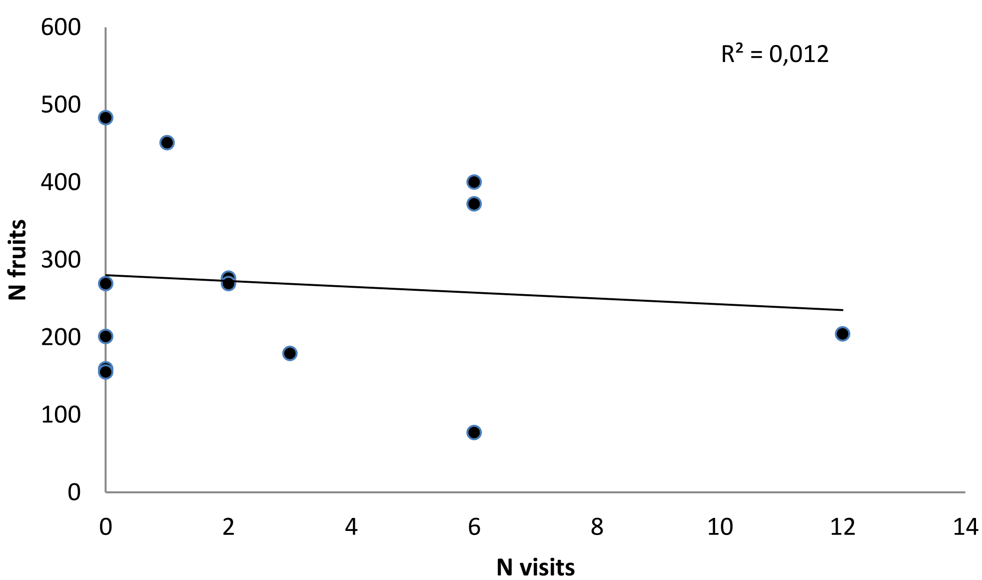

Figure 10 – Correlation between number of fruits and number of visits in different *Marcgravia longifolia* individuals

In Fig 11, the association between the number of visitors, consumers, and fruits consumed per observation session is displayed. Concerning ID17, only two observations were carried out, while in ID32 few visitors were recorded and therefore, these individuals are not shown.

For ID22, no visitors were counted on the first observation but on the second, one visitor entered the *Marcgravia* and fed on one fruit. On the third observation, no fruits were eaten by the only visitor counted.

The main consumers observed in the total of all *Marcgravia* individuals were *Dixiphia pipra*, the species with the highest records of feeding events, consuming in total 109 fruits, and *Tangara chilensis* with a total of 72 fruits (Fig 12). *Dixiphia pipra* was also the most frequent visitor, while *Tangara chilensis* came in fourth place. Visits of *Tangara chilensis* might have been underestimated due to the fact that *Tangara* species travel in flocks, and are thus, more difficult to identify, while manakins forage solitarily. On the other hand, manakins are easier to identify as they feed at intermediate levels, while other species converge to the canopy.

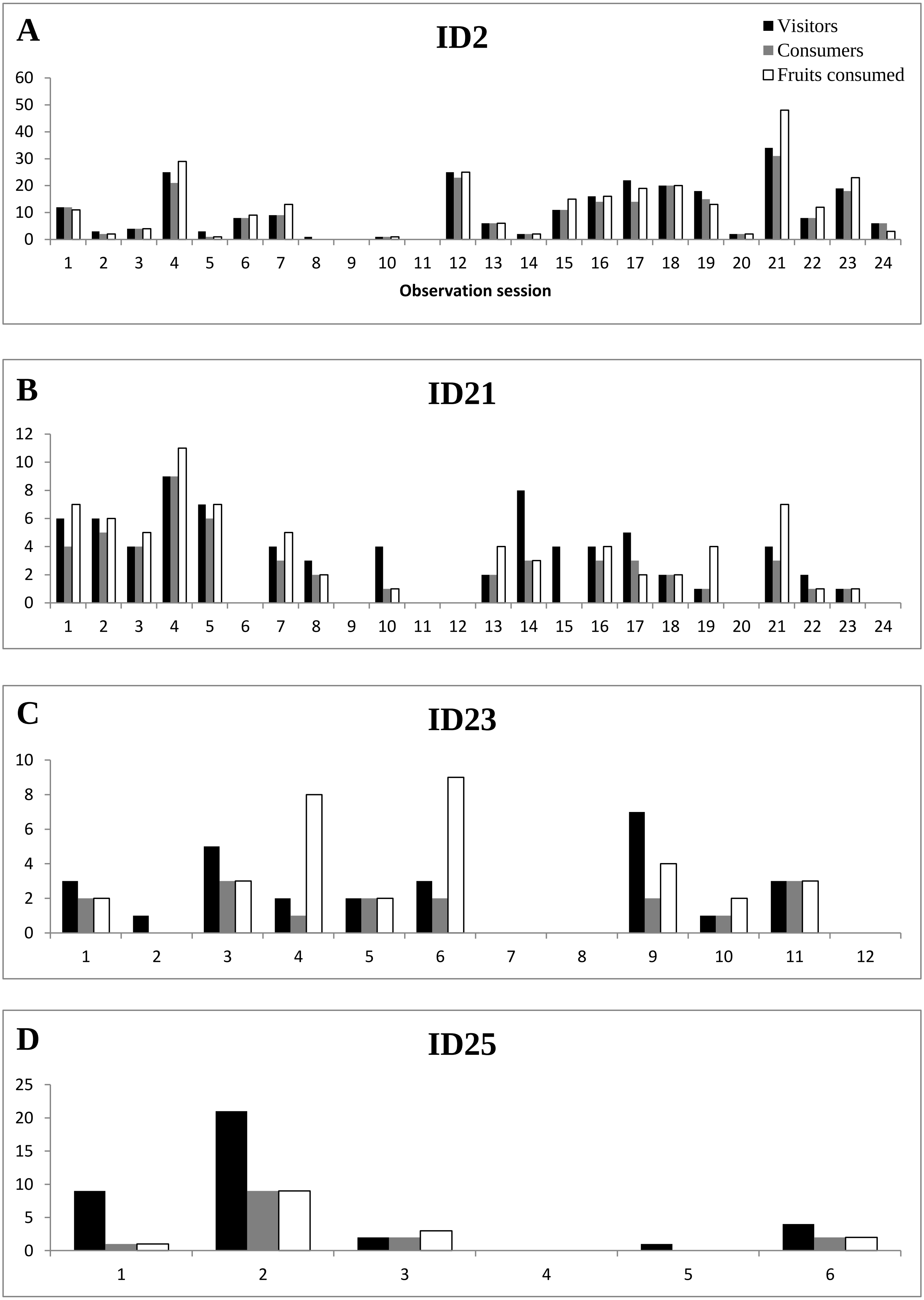

Figure 11 – Number of visitors, consumers and fruits consumed in different *Marcgravia longifolia* individuals

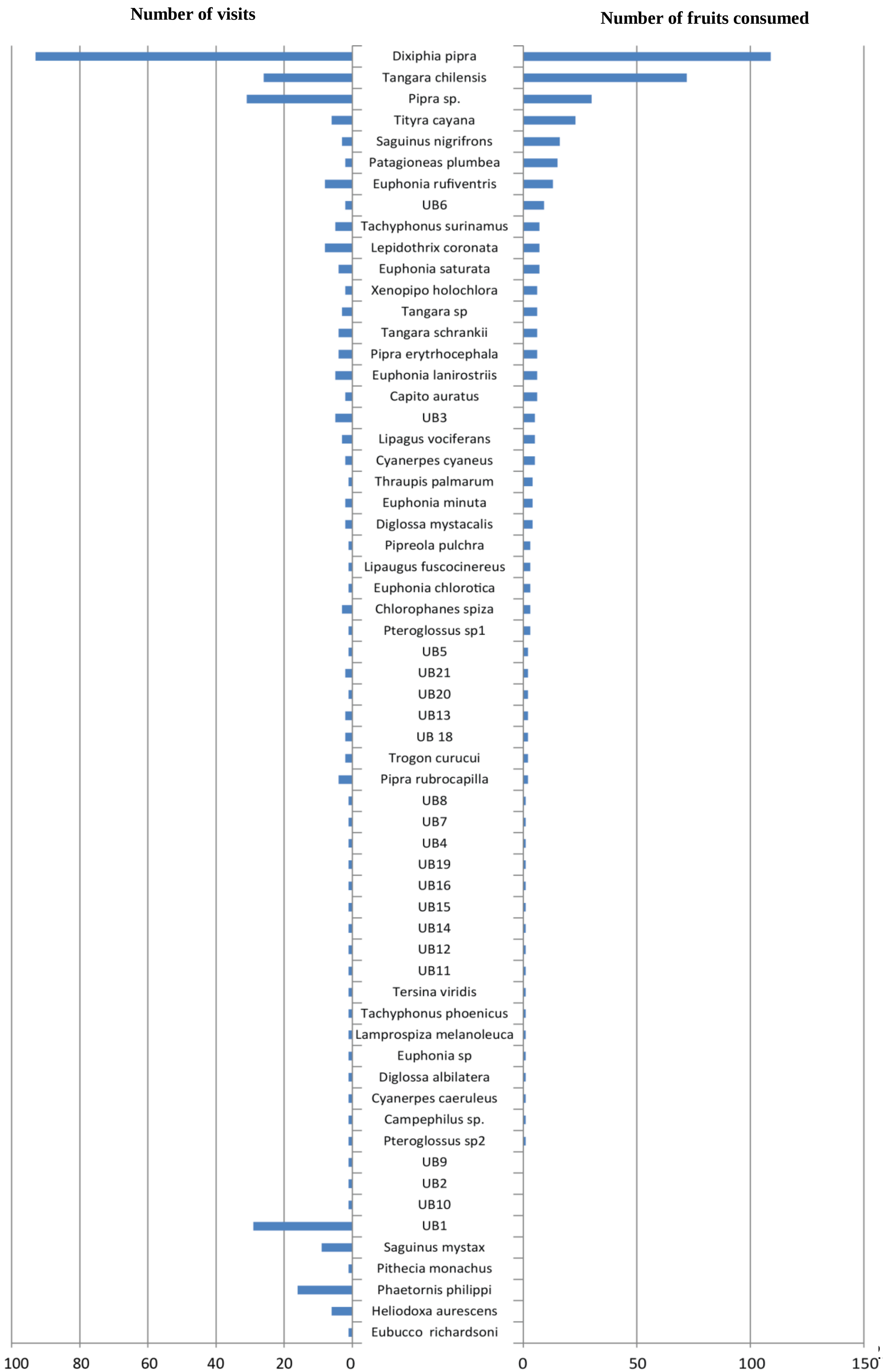

Figure 12 – Relation between number of visits and fruits consumed by different species at different *Marcgravia longifolia* individuals

3.3 Phenology

3.3.1 Inflorescences & Infrutescences counting

Means and standard deviations of the number of inflorescences and nectaries counted till three meters high in seven *Marcgravia longifolia* individuals are shown in Table 3. A single counting per individual, performed at the beginning of the study, was used for these calculations.

Table 3 - Mean; Standard Deviation and range of inflorescences, flowers and nectaries of *Marcgravia longifolia*

	Mean	SD	Range
Number of inflorescences	2.1	2.3	0 - 5
Number of flowers per inflorescence	23	11.4	0 - 34
Number of nectaries per inflorescence	3.7	1.8	3 - 6

Figure 13 – *Marcgravia longifolia* inflorescence with closed flowers and nectaries

Figure 14 – *Marcgravia longifolia* inflorescence with open flowers during the night

Infrutescences (Fig. 15 and Fig. 16) were more prevalent than inflorescences and the number of fruits per infrutescences was also high (Fig. 17). Both were highly variable amongst *Marcgravia* individuals.

Figure 15 – *Marcgravia longifolia* infrutescence with a ripe fruit dropping the husk and unripe fruits.

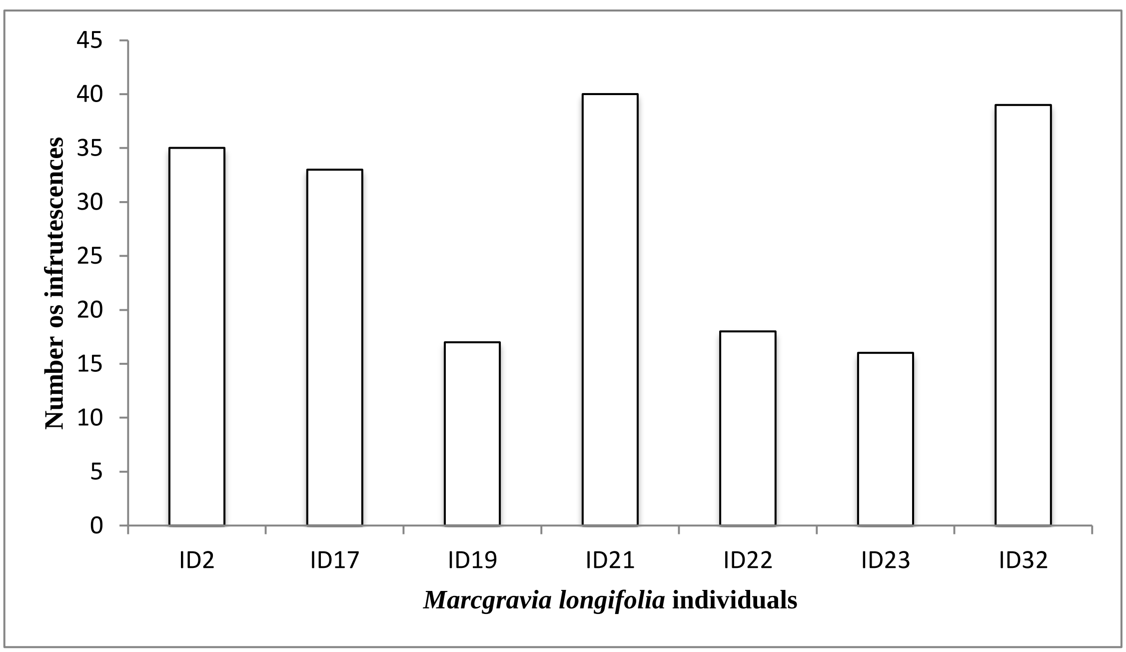

Figure 16 – Number of infrutescences of *Marcgravia longifolia* individuals

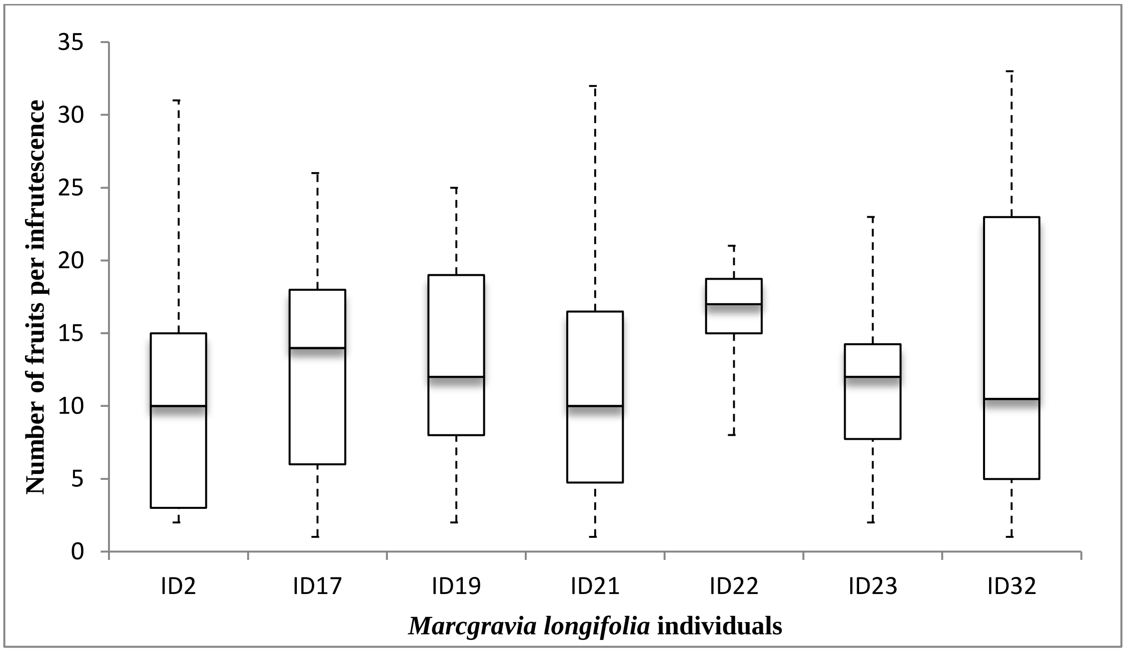

Figure 17 – Number of fruits per infrutescence of *Marcgravia longifolia* individuals. Box plots show the median, and the quartiles 25 and 75; outliers are indicated by the dashed lines.

In order to estimate the crop size of the *Marcgravia* individuals, an extrapolation was performed by multiplying the observations made previously by the total height of the liana (Table 4). It should be noted that since fruit abundance might be different near the canopy, this consists of a rough estimation, although important to have an insight on the productive capacity of an individual. It is displayed also a mean number from each individual, since with time passage the productivity decreased and some individuals remained without any fruits in the first 3m.

Table 4 – Phenological data of seven different *Marcgravia longifolia* individuals

ID	Height (m)	DBH host (m)	Mean number of fruits per 3m	Maximum number of fruits per 3m	Total number of fruits per liana
2	32	5.55	97	319	3402
17	23	1.05	136	422	3235
19	24	0.8	116	220	1760
21	18	1.30	252	457	2742
22	25	2.10	140	294	2450
23	25	1.90	77	182	1516
32	32	2	225	535	5706

3.3.2 Fruit mass and chemical content

In order to study fruit composition, a total of 21 fruits from 3 different *Marcgravia longifolia* individuals were collected for mass determination. The mean mass of the fresh fruits was of 0.67 g (SD = 0.33). In only a couple of days, after incubation in silica, their mass was in general reduced to less than half of their original weight (0.20 g SD = 0.10) which reflects their high water content (Fig.18). Since *Marcgravia longifolia* seeds are small (approximately 1mm) and present in thousands, it was unfeasible to separate them from the pulp and therefore, the dry weight calculation also includes seeds.

Their relatively low dry mass is also due to the fact that *Marcgravia longifolia* fruits carry a low content of Acid Detergent Fiber (ADF) and Neutral Detergent Fiber (NDF): 6.4% and 12.2%, respectively, as determined by Ripperger *et al*. 2014 These are defined as the fraction of the fruit cells' wall that is composed by cellulose and lignin (ADF) and by the previous plus hemicellulose (NDF). Both are inversely correlated with digestibility.

Figure 18 – Difference between fresh fruits (bottom ones) and dry fruits of *Marcgravia longifolia*

In order to determine sugar concentration, 17 fruits derived from 5 different *Marcgravia longifolia* individuals were analyzed. The mean sugar level was 24% (SD = 2.3) in a range of 18.5% – 29.2% which constitutes a high sugar content.

3.3.3. Fruit loss estimation

In order to determine the amount of fruits lost by *Marcgravia longifolia* individuals, net traps were checked during 49 days (Fig. 19). In total, 510 fruits were counted at the nets surveyed in the morning (Fig 20) and 289 at the nets checked in the evening (Fig. 21). The graphics show the difference between the fruit number in the two different times of the day according to their ID. It is clear that in the morning, more fruits were encountered than in the evening and that fruit loss decreased towards the end of the study due to lower productivity of *M.longifolia* individuals.

Figure 19 – Net traps placed under a *Marcgravia longifolia* individual

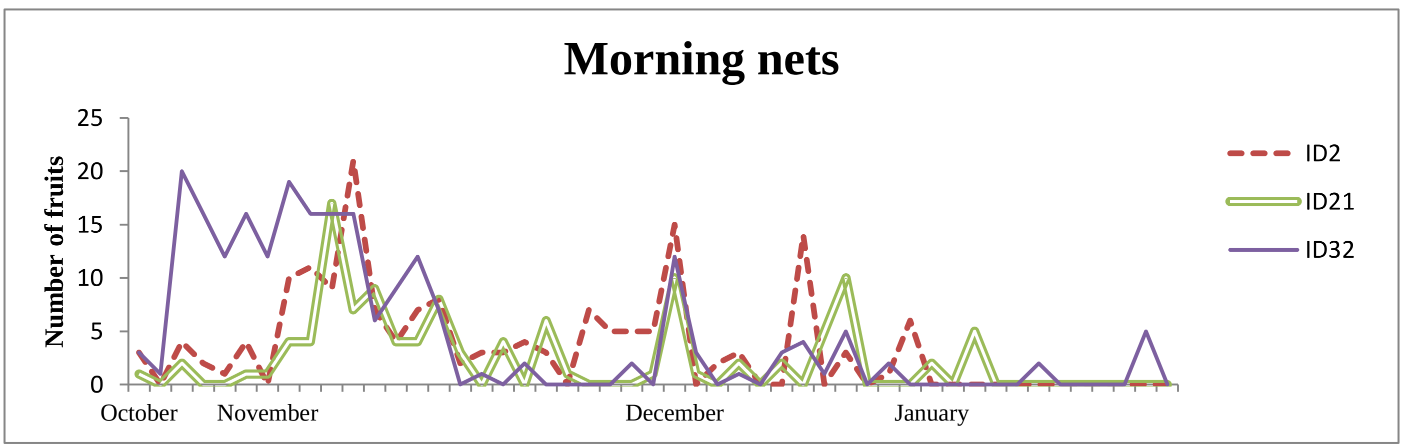

Figure 20 – Fruit loss from the nets checked early in the morning

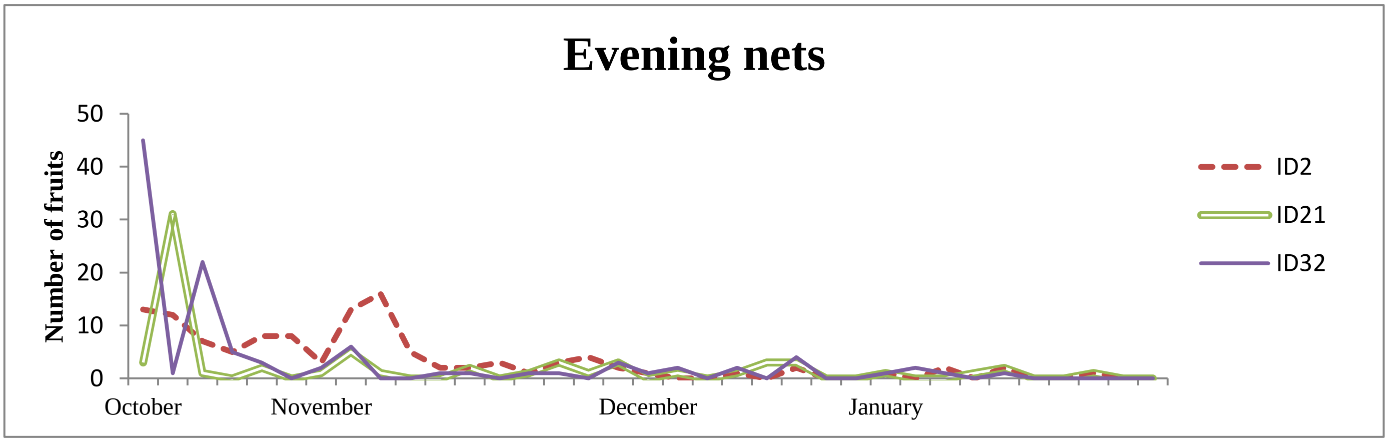

Figure 21 – Fruit loss from the nets checked late in the evening

3.4 Host specificity

3.4.1 Host preference

From the total of 49 *Marcgravia longifolia* individuals, 36 hosts were identified until family and genera (Table 5). Due to the tree height of some individuals, lack of leaves at the canopy or bad visibility (which difficult the observation with binoculars) the rest of the hosts remained unidentified.

Using the Ecological Methodology software, a test for Resource Selection was performed using the inventory of Dávila & Ríos (2006) as potential hosts prevalence was compared with the actual hosts identified during the study. This estimation was done, based both on family and Genus to overcome variability between different botanists in species identification. The software uses Manly *et al*. (1993) G-test to check the null hypothesis that *Marcgravia* individuals are selecting hosts randomly. Manly's α is also referred to as Chesson's Index, and it is strongly affected by the values observed for rare resource items and by the number of resource types used in a study (Confer & Moore 1987).

In total, in the inventory used as a reference, there were 44 families identified with 1084 individuals corresponding to 137 genera identified with 1057 individuals. For the current study, all families and genera with only one individual were excluded from the analysis since the probability that *Marcgravia longifolia* would colonize one of those is extremely reduced. Therefore, the final number of families was 39 with 1079 individuals and 91 genera with a total of 1011 individuals.

Table 5 – Identified hosts of 36 *Marcgravia longifolia* individuals

Family	Genera	Host number of *Marcgravia* individuals
Burseraceae	*Protium*	2
Chrysobalanaceae	*Couepia*	1
Combretaceae	*Bouchenavia*	1
Elaeocarpaceae	*Sloanea*	1
Euphorbiaceae	*Hevea*	1
Fabaceae	*Hymenaea*	1
	Macrolobium	1
	Parkia	2
Humiriaceae	*Vantanea*	1
Lecythidaceae	*Eschweilera*	18
Meliaceae	*Guarea*	1
Moraceae	*Brosimum*	1
Myristicaceae	*Iryanthera*	1
	Virola	1
Olacaceae	Unidentified	1
Quiinaceae	*Quiina*	1
Sapotaceae	*Manilkara*	1

The software calculated the probability of accepting the null hypothesis (random choice of hosts by *Marcgravia longifolia*) which resulted in 75% of acceptance regarding genera and 42% for family. This outcome supports that *Marcgravia longifolia* hosts are probably chosen according to the availability of the different host species and not due to some intrinsic preference factor.

3.4.2 Potential hosts of *Marcgravia longifolia*

Since rarefaction is a statistical method for estimating the number of species expected in a random sample of individuals taken from a collection (Krebs 2014), rarefaction curves were calculated with the aim of estimating how many potential genera and families could constitute hosts for the 36 *Marcgravia* individuals where hosts were identified.

Displayed on Fig. 22 is the result when taking into account genera. When crossing the x axis value 36 (the number of identified hosts in *Marcgravia* individuals) with the corresponding y axis, the matching number of potential hosts is approximately 60. This result is quite representative of the total number of genera existent in the inventory when excluding the rare genera (91 genera). Regarding families (Fig. 23), 32 potential families could host *Marcgravia longifolia*, which is a good representation when taking into account the total number of families in the inventory (44). If compared with the number of families excluding rare ones, as done previously with genera, the representation is even stronger (39 families).

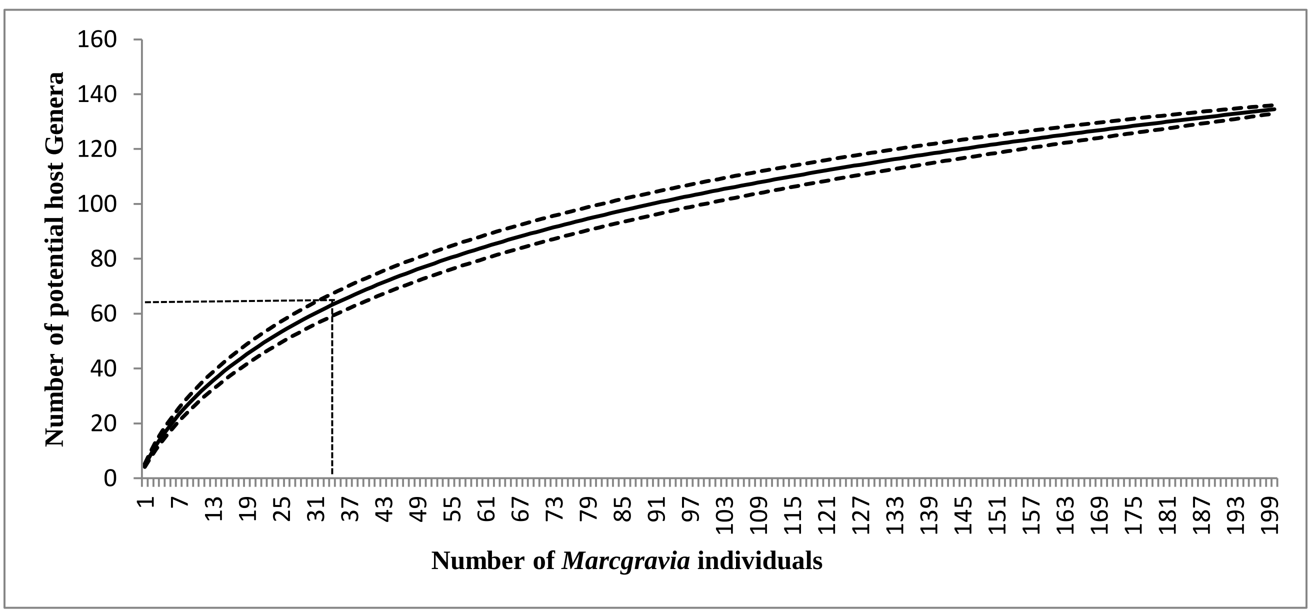

Figure 22 – Rarefaction curve of potential Genera hosts of *Marcgravia longifolia*

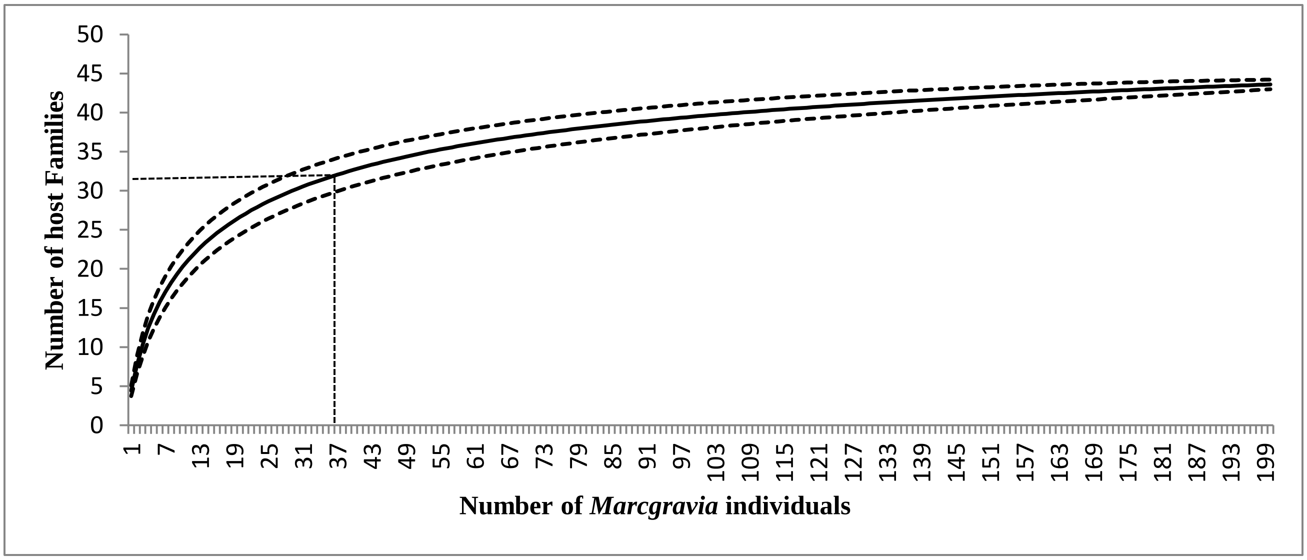

Figure 23 – Rarefaction curve of potential Family hosts of *Marcgravia longifolia*

3.4.3 Host diversity

In order to calculate the diversity of potential genera and family hosts, different estimations were performed based in different indexes (Table 6).

One of the most popular indexes of species richness used in ecological studies is Shannon's H'. The results regarding this index were 5.71 for genera and 4.42 for family. When using Simpson's Index, (range between 0 and 1) the greater the value the greater the diversity, meaning that diversity can be considered high in both cases, genera and family (0.95 and 0.93 respectively).

In evenness measures, indexes range from 0 to 1 as well, with the highest value meaning a complete equitability/evenness of the distribution. Despite all results showing a low equitability, implying a numerical unequally inventory, Smith and Wilson's Evar was the index that had a more equilibrated result regarding genera, probably due to the independence of species richness and due to the sensitivity of both common and rare taxa.

Table 6 - Diversity indexes of Genera and Family hosts of *Marcgravia longifolia*

		Genera	Genera (excluding rare)	Family	Family (excluding rare)
Measures of Heterogeneity	Simpson's Index	0.95	0.95	0.93	0.93
	Shannon's H'	5.71	5.45	4.46	4.42
	Brillouin's H	5.42	5.21	4.34	4.31
Measures of Evenness	Camargo E'	0.33	0.40	0.37	0.41
	Simpson's E	0.17	0.23	0.34	0.38
	Smith and Wilson's Evar	0.40	0.51	0.29	0.38

4. Discussion

4.1 *Marcgravia longifolia*, a Keystone resource?

Defining Keystone Plant Resources can be a difficult task. The parameters used to identify keystone plant species in tropical forests can include different categories. According to Peres (2000), the following variables can be used to define a KPR:

1) Temporal redundancy [TR] – Availability of a potential resource comparing to the alternative food resources. It may range from entirely indispensable, if it becomes available during periods of fruit scarcity, to completely substitutable if it turns out to be available only during the months of peak availability of all alternative plant resources consumed.

2) Degree of consumer specificity [CS] – Inverse function of the frugivorous percentage that was reported to exploit a possible KPR. Therefore, resources could range between extremely generalized, if they were being consumed by at least one half of the frugivorous species community to extremely specialized, if they were consumed by only 5% or less from the frugivorous community.

3) Resource reliability [RR] – Availability of a resource at a given site during scarcity periods to sustain the vertebrate community. The phenological variation of a plant resource may range from an extremely unreliable supraannual resource, if it fails to become available in more than 50% of years, to extremely reliable, never failing to turn out available at least once per year.

4) Resource abundance [RA] - The coarse abundance of a potential KPR at a particular location, on the basis of the approximate patch density of a given resource and, when available, some indication of patch size (e.g. crown volume). In these terms, a medium-sized plant resource may range from extremely rare if it occurs at densities of ≤ 1 patch km^{-2}, to superabundant, if it occurs at densities of ≥ 250 patches km^{-2}

Therefore, from a consumer perspective, keystone plants would be defined as those producing highly reliable resources with low-redundancy that are consumed by a great proportion of the vertebrate assemblage. Nevertheless, there is little agreement on the proportion of local vertebrate assemblage that a plant species must serve during critical times of the year before it can be recognized as a keystone resource. Some studies have even identified KPR with few consumers such as one or two species (Overdorff 1992; van Roosmalen 1985).

Another parameter that should also be taken into account, relates to the degree of taxonomic treatment given to the relevant plant taxa. For instance, all epiphytes in a given forest could be considered as an aggregate keystone resource because they add to the forest structural complexity and contribute to ecosystem processes such as nutrient cycling (Nadkarni 1994).

Considering all these differences amongst concepts between authors, we propose that *Marcgravia longifolia* constitutes a likely candidate for a keystone resource. The most important trait is the peculiarity of producing fruits throughout the entire trunk level, thereby it can be a resource for different vertebrates at different strata. This is an extremely important trait, due to the existence of vertical patterns in the distribution of bird, primates and other mammals. Additionally, *Marcgravia longifolia* fruits produces highly nutrient rich fruits and for instance, it could be speculated that the fruits located in at higher levels of the plant could be even richer in nutrients. A recent study supports vertical stratification of fruit nutrients as sunlight, humidity and temperature also vary within the tree level (Houle *et al*. 2014). Moreover, the fact that *M. longifolia* produce fruits throughout the dry season (although in lower numbers than in the main fructification period) makes it a reliable species. Furthermore, a high number of fruits are produced per individual and with an asynchronous fructification. Additionally, there is a high number of *Marcgravia* individuals distributed throughout the field station, which is an important aspect for supporting the vertebrate community.

Observations demonstrated that 17% of the bird community that composes the study area visited *Marcgravia longifolia*. The bird community is defined from an inventory done in Quebrada Blanco by Lars Pomara, where circa 324 bird species were identified. The latter though, requires a careful interpretation when compared to the results presented here, since not all species that compose it include fruits in their diet or live in the same habitat where *Marcgravia longifolia* is present (non-flooded areas). When excluding species that were observed but that whose range does not include EBQB (as determined with the aid of field guides), the percentage of visitors only drops to 14%, which is still a significant proportion of the bird community of the study area.

Since a keystone could be simple defined as an `animal or plant species with a pervasive influence on community composition' (Howe & Westley 1988),*Marcgravia longifolia* would be a fine candidate for this classification, at least in a regional scale, due to the ecology and importance in the diet of a big fraction of the bird community.

4.2 *Marcgravia longifolia* distribution

Frugivory and animal seed dispersal are important processes in forest ecosystems (Şekercioğlu 2006). In tropical forests, up to 90% of the plant species produce fleshy fruits that are eaten by animals (Howe & Smallwood 1982). Frugivorous animals, in particular birds, rely on fruits as a key source of energy (Kissling *et al.* 2009) and provide seed dispersal for plants with fleshy fruits. Regarding the feeding habits of the frugivore community, fruit removal will not only depend on the traits of the species, but also on the surrounding environmental context, which is often shaped by the occurrence of other plant species (Carlo *et al.* 2007).

When analyzing the population of *Marcgravia longifolia*, there was evidence of clustering amongst individuals. This could be due to the dispersers' assemblage, which can vary within the field site and for instance, disperse seeds at the next *Marcgravia longifolia* or in between individuals. Manakins, were the ones with higher feeding records on *Marcgravia longifolia* fruits, which makes them likely candidates for main dispersers of this liana. These results are in accordance with previous reports that have shown that manakins are the primary seed dispersers of many shrubs and treelets in tropical forests (Loiselle & Blake 1999) and that variation patterns in fruit handling behavior and species abundance can affect seed dispersal (Jordano & Schupp 2000). These observations can be related with the clustered distribution of *Marcgravia longifolia* individuals. Furthermore, adult male manakins, due to their attachments to lek sites, are more sedentary (i.e. smaller home ranges) as compared to females and young males (Lill 1974, Graves *et al*. 1983). This feature, implies that male manakins do not disperse seeds as widely or into as many microhabitats as do females and young males (Krijger *et al*. 1997). However, this is only observed during the breeding season; otherwise male manakins move through much wider areas (Théry 1992).

During focal observations, the proportion of male manakins was of 47% while females accounted for 53% of observations. These percentages should be treated with prudency, since young individuals can be easily misidentified as females, leading to biased distribution of gender. Another study with a lekking species (*Cephalopterus penduliger*) has showed that males deposit the seeds mainly within the lek, while females deposit more evenly across the landscape (Karubian *et al*. 2012).

Many species of manakins are heavily dependent on fruits (Levey 1988, Loiselle & Blake 1990; Marini 1992). Fruit abundance varies markedly in space and time (Loiselle & Blake 1994, Rosselli 1994) and, consequently, abundances of manakins are hypothesized to exhibit temporal and spatial variation in use of habitats (Martin & Karr 1986; Levey 1988; Loiselle & Blake 1991).

Marcgravia longifolia distribution may also be connected with fruiting neighborhood. This, is an important driver for selection of trees as feeding resources by vertebrates, and spatial context around an individual plant may have important consequences for different processes (i.e. facilitation, competition and pollination). The influence of neighboring trees over frugivore visitation and fruit consumption may generate mutualistic and competitive processes with the potential to shape tree recruitment and community dynamics (Sasal & Morales 2013). Likewise, the dense neighborhoods attract more birds and keep them away from isolated plants and/or low density neighborhoods thus increasing inequalities in fruit removal (Carlo & Morales 2008). Fruiting neighborhood, may be an explanation for the low visitation rates to the ID 32, where one would expect the opposite, due to the high productivity and crop-size (the individual with highest fruit numbers). It remains as an interrogation, if the low visitation numbers are due to the unattractive surroundings or/and due to changes in the frugivore community, as no study was done regarding the vertebrate community or neither an inventory to the plant species diversity in the entire study area (100 hectares).

4.3 *Marcgravia longifolia* phenology and fruit quality

Marcgravia longifolia has an asynchronous fructification, fruits and flowers are permanently available throughout the year within the community. Nevertheless, a fructification peak generally occurs between September and December. During data collection, the availability of fruits decreased more rapidly than observed in previous years by field assistants. This situation could be due to changes in the fructification period, which might have started earlier, and/or due to a major influence of climatic factors. The latter were found to be highly related to phenological patterns in plants, of which temperature and rainfall are the most commonly, referred to. While temperature is more often related to phenology in temperate forests (Fitter *et al*. 1995), rainfall exerts a more significant effect in tropical forests (Borchert *et al*. 2004). During the study period there were phases with intense rain which could have accelerated fruit maturation. Despite the previous, the differences might also be attributed to variability of fruit availability between years.

Phenological patterns of variability can also be related with functional plant traits, such as seed dispersal syndromes which can affect the community function and assembly. There is a relationship between dispersers and fruiting patterns, where it was shown that some plant communities display different periods of fructification that could be associated with certain dispersal syndromes. In tropical forests it has been observed that plants with seeds dispersed by frugivorous animals tend to bear ripe fruits during the wet season, whereas in the dry season the wind dispersed species prevail among the fruiting species (van Schaik *et al*. 1993).

The fruit selection by potential seed dispersers may depend on several factors such as fruit abundance, accessibility, competition, predation risks, fruit size, color, and secondary compound content (Murphy 1994). Nevertheless, it is commonly accepted that generally, dispersers prefer nutrient-rich ripe fruits over unripe fruits with low nutritional value (Schafer 2003). For manakins, fruit nutrient content is quite important especially during the mating season, due to their lekking courtship behavior, where males show complex display behavior to attract females (Sick 1967 and Prum 1990). This carries a high energy cost for males, due to their large investments in attending the lek and competing for female visitors, which implies less time for foraging or other maintenance activities.

Fruits with high nutrient content are important all year round for the frugivore community, especially when there is food scarcity. Birds due to the lack of fruits or ripe fruits might feed on unripe fruits (Leck 1972). This can be particularly problematic for manakins, since they need to consume 6.6 times as many unripe fruits than ripe fruits to satisfy their energy demands (Foster 1977).

Marcgravia longifolia fruits, having a high level of sugar concentration, lipids and proteins are a good resource for the frugivore assemblage. However the nutritional rewards of the fruits also attract antagonists, which consume fruits without providing any benefit to the plant. Due to this, plants developed a strategy to deter the consumption of their fruits by undesirable species or pathogens that involves the production of secondary compounds. *Marcgravia longifolia* fruits have been analyzed by Ripperger *et al*. 2014 where fruits derived from 13 different plant species where examined: five fruits were commonly eaten by bats, five by both tamarins and bats (where *Marcgravia longifolia* is included) and three by only tamarins. The sugar concentration of *Marcgravia longifolia* fruits was amongst the highest (68.7% in a range of 7.3 % – 84.4%). Additionally, it was the fruit with the highest level of soluble protein (13.42%, range: 0.89% to 13.42%), and the second in lipid content (6.44%, range: 0.72% - 32.89%). Interestedly, it also possessed a high content of phenolics (7.98%, range: 0.3% - 7.98%) and condensed tannins (4.04 %, range: 0.11% - 4.07%).

Fruit secondary compounds, may have a significant effect on frugivore preference. For instance, phenols and tannins have been widely adopted as feeding deterrents because they can interfere with protein digestion (Robbins 1993) and are associated with food taste (Rosenthal & Janzen, 1979). Since frugivory can be beneficial or detrimental to plants, the evolution of fruits and flowers is assumed to respond to the amount of selective pressures from mutualists and antagonists (Whitney & Stanton 2004).

The defense trade-off hypothesis is amongst the most influential theories about secondary compounds in ripe fruits, it assumes that there is a trade-off between defense against damaging agents and palatability for dispersers. There are two alternative models of this hypothesis, the *removal rate model*, that predicts the existence of an inverse relationship between nutrients and secondary compounds, since nutrient rich fruits should be quickly removed and therefore require fewer defenses. On the other hand, the *nutrient/toxin model* that assumes a positive correlation between nutrients and secondary compounds, since nutrient-rich fruits should be profitable enough to allow for the retention of higher levels of defense (Cipollini & Levey 1997b).

The first model is supported by different studies (Cipollini & Levey 1997a; Shaefer *et al*. 2003, Cazzeta *et al*. 2008), but there are some doubts if it can be applied to *Marcgravia longifolia*. The studied fruits had not only a high nutrient content but also a high level of metabolites (defenses), which means that the inverse relationship is not applied in this case. However all fruits collected for analyzes were from less than two meters height, and if one speculates about vertical stratification within the same individual on fruit richness, the fruits from higher levels could be more nutritious but with low levels of defense. If so, the model could be accepted as candidate to explain *Marcgravia longifolia* secondary compounds. Alternatively, in the second model, fruits are attractive enough to overcome the detrimental effects of metabolites. Since birds have a high tolerance for many classes of secondary compounds, which could be deterrent or even toxic to mammals (Tewksbury & Nabhan 2001), and considering they are the main dispersers of this liana, secondary compounds could be seen as a preventive strategy to discourage mammals to feed on *Marcgravia longifolia*, avoiding in this way undesirable consumers.

4.4 *Marcgravia longifolia* hosts

Numerous factors have been suggested to influence liana host selection. Climbing mechanisms frequently dictate which host trees lianas can climb (Peñalosa 1982). Normally, lianas with particular adhesive structures (aerial roots, adhesive discs) can climb nearly any host large enough to support their weight (Putz 1984, Carter & Teramura 1988). Furthermore, larger hosts and those with already liana presence are more likely to be colonized (Putz 1984, Nabe-Nielsen 2001). Normally, bark texture relates to liana climbing success with fewer lianas on trees with smooth bark and more lianas on irregular bark which provides attachment points for climbing (Putz 1980, Campanello *et al*. 2007).

Regarding tree species diversity at EBQB, it is mainly dominated by the Lecythidaceae family and afterwards by Fabaceae. Lecythidaceae has a Pantropical distribution, and contains approximately circa 17 genera and 300 species. The greatest diversity of this group occurs in the Neotropics especially in the Amazon region and the Guianas (Mori & Prance 1990). These plants occur in various environments but are most common in non-flooding primary forests (Mori & Prance 1990) and are considered indicators for preserved or little-disturbed areas (Mori *et al*. 2007). In EBQB, the most common genera belonging to Lecythidaceae family is called *Eschweilera*, which possesses the peculiar characteristic of presenting regular bark shedding. This genera is also the most common host used by *Marcgravia longifolia*, which is unusual, due to the bark feature of Eschweilera individuals.

4.5 Field constrains

Some constrains during the field work were encountered and are discussed here:

- The study was initiated in mid-October, when normally the infrutescence peak initiates in September, and thus, a part of the fructification period was lost. Secondly, since the work was conducted during the rainy season, there were periods where focal observations and phenological work were suspended, due to heavy rain/storms.
- No focal observations were performed during night to study nocturnal frugivores, which could have enriched our knowledge on *Marcgravia longifolia* visitors.
- Additional information could have been collected on bird abundance and feeding habits, plus their capacity for dispersion of *Marcgravia longifolia*, but this would require longer periods of observation and additional resources.
- A larger period of observations would be required to collect additional data that would support the identification of all *Marcgravia longifolia* hosts, as well as to monitor fruit production and availability by this liana in different seasons.
- Due to the station isolation from any village with no food resources nearby, there was a need to return to the nearest town (Iquitos) every three weeks for the purchase of provisions and thus, no field work was performed in those days.

5. Conclusion

Lianas, do not only add to the structural complexity of forests, but can have a major role in the ecosystem since they comprise up to 40% of woody individuals and species in tropical forests (Gentry 1991, Schnitzer & Bongers 2002). In Cocha-Cashu Biological Station in Peru, nine of the 21 potential KPR are lianas (Diaz-Martin *et al.* 2014). Since KPR may set the carrying capacity of a frugivore assemblage (Terborgh 1986a) their identification and characterization are of great importance for the creation of conservation strategies.

This work made a step forward regarding the knowledge available on *Marcgravia longifolia*. This rather unknown species possesses the peculiarity of producing a high number of fruits from low levels to the canopy, being able to deal with different vertebrates at different strata. Besides, due to their high nutritional content, its fruits can constitute an excellent resource for the local assemblage, and this probably justifies why a large fraction of the bird community was seen feeding on this liana. Taking into account all features mentioned, it is plausible to conclude that *Marcgravia longifolia* exerts an important role within EBQB ecosystem being a possible candidate to a KPR, at least in a regional scale.

It is also important to underline, that the keystone status of a species is entirely context-dependent. Different ecological conditions may lead to different roles of species within a community (Menge *et al*.1994, Navarrete & Menge 1996), and the role that *Marcgravia longifolia* has on the EBQB might not be replicated in other areas. Community structure defines species importance and its contribution to the environment, and this is of paramount importance when defining keystone species.

In conclusion, *Marcgravia longifolia* due to all features presented might have an important role in EBQB community, and its preservation might be essential for the balance of the local assemblages and ecosystem.

6. Conservation implications

Key Plant Resources may influence the frugivore assemblage and affect the way communities interact due to their food supplies during scarcity periods.

Being so, it is vital to increase the information about specific candidates when selecting or monitoring areas of conservation interest. Since *Marcgravia longifolia* is an epiphytic liana, it requires hosts where to grow on, being affected directly if those host species are not present. Individuals from the genera Eschweilera are common hosts, (locally known as Machimango) and are used by humans due to their wood quality and logged from various places in tropical areas (as well as the majority of the other hosts used by *Marcgravia longifolia*). If there are no policies to protect these species, a cascade effect could occur, first affecting *Marcgravia* and after the frugivore community, thereby altering the dynamics of the vertebrate assemblage at a regional scale. At a global scale, Eschweilera, due to the bark shedding peculiarity, is used by native populations from the Colombian Amazon to build torches and traditional objects (Acero 1979). Therefore, logging will not only affect the frugivore community, but also the local populations that use this specie for their own benefit. Furthermore, it is common in logging operations that lianas are cut in order to reduce biomass and increase tree growth rate and commercial values of the host species (Putz 1991). *Marcgravia longifolia* could be further affected by these operations. As such, there is an urgent need to create new strategies and policies to protect both vertebrates and plant communities due to their mutualistic relationship, straightly connected with the ecosystem equilibrium.

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Appendix

Table 7 – GPS coordinates of the different *Marcgravia* individuals at EBQB

ID	GPS COORDINATE	OBSERV
2	18M 0704461 UTM 9517814	
3	18M 0704620 UTM 9517729	
4	18M 0704661 UTM 9517725	
5	18M 0704672 UTM 9517745	
6	18M 0704712 UTM 9517761	
7	18M 0704813 UTM 9517847	
8	18M 0704801 UTM 9517703	
9	18M 0704891 UTM 9517731	
10	18M 0704954 UTM 9517640	
11	18M 0704951 UTM 9517740	
12	18M 0704917 UTM 9517962	
13	18M 0704909 UTM 9518230	
14	18M 0704756 UTM 9518034	
15	18M 0704618 UTM 9518010	
16	18M 0704034 UTM 9518114	
17	18M 0704030 UTM 9518131	
18	18M 0703990 UTM 9518042	Other specie
19	18M 0704030 UTM 9517967	
20	18M 0703869 UTM 9517928	
21	18M 0704395 UTM 9517925	
22	18M 0704500 UTM 9517900	
23	18M 0704490 UTM 9517891	
24	18M 0704600 UTM 9517921	Other specie
25	18M 0704143 UTM 9517760	
26	18M 0704209 UTM 9517687	
27	18M 0704247 UTM 9517709	
28	18M 0704287 UTM 9517709	
29	18M 0704107 UTM 9518484	
32	18M 0704392 UTM 9518115	
34	18M 0704547 UTM 9517910	
36	18M 0704100 UTM 9518085	
37	18M 0704947 UTM 9518073	
38	18M 0704897 UTM 9518088	
39	18M 0704914 UTM 9517970	Probably dead
40	18M 0704503 UTM 9517616	

41	18M 0704507 UTM 9517613	Other specie
42	18M 0704179 UTM 9517551	
43	18M 0704176 UTM 9517559	
44	18M 0704172 UTM 9517594	
45	18M 0705003 UTM 9518014	
46	18M 0704199 UTM9517794	
47	18M 0704046 UTM 9517998	
48	18M 0704288 UTM 9518187	
49	18M 0704802 UTM 9517760	
50	18M 0704099 UTM 9517950	
51	18M 0704016 UTM 9517982	
52	18M 0704380 UTM 9518143	
53	18M 0705030 UTM 9517851	
54	18M 0705062 UTM 9517827	
55	18M 0705155 UTM 9517750	
56	18M 0705037 UTM 9518047	
57	18M 0705044 UTM 9517859	